

## Liana avoidance strategies in trees: combined attributes increase efficiency

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**Abstract:** We investigated the importance of specific tree attributes: height, exfoliating bark, smooth bark, and fast growth to determine whether single or multiple attributes were more important in liana colonization on trees. Specifically we asked: Does the presence of multiple liana-shedding attributes in trees reduce the number of lianas on a tree? We sampled the number of lianas on each tree and recorded tree attributes in three ecologically distinct sites in southeast Brazil. Data were analyzed using model selection by Akaike Information Criterion, in which the number of lianas on a tree was the response variable and tree attributes were explanatory variables. We found that a combination of two attributes in trees was sufficient to deter liana infestation, whereas only one attribute had zero probability of deterring lianas across all sites. Taller trees bear more lianas, probably because of their well-lit canopies, but tree height was always associated with other attributes: slow growth in rain forest, exfoliating bark in seasonal forest, and rough bark in savanna woodland. We conclude that the presence of two attributes is sufficient to reduce liana infestation on a tree.

**Key words:** Akaike Information Criterion, cerrado, climber, host-tree, liana infestation, rain forest, savanna, seasonal tropical forest.

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### Introduction

Lianas (woody climbers) are well-represented in tropical forests, particularly in seasonally dry tropical forests (DeWalt *et al.* 2009; Schnitzer 2005). The effects of lianas on trees are generally negative, because lianas can reduce tree fruit production (Fonseca *et al.* 2009), inhibit tree growth (Clark & Clark 1990), and increase tree mortality (Grogan & Landis 2009). Some attributes (*sensu* Vielle *et al.* 2007) of trees may deter liana growth

and colonization (Hegarty 1991), thereby avoiding harmful effects.

Fast-growing tree species bear fewer lianas than other species (Campanello *et al.* 2007; Carse *et al.* 2000; Clark & Clark 1990) possibly due to their shorter lifespan (Clark & Clark 1990). Tree bark characteristics also can play an important role in liana avoidance: trees with exfoliating bark have fewer lianas (Campanello *et al.* 2007; Talley *et al.* 1996) because the regular renewal of the outer bark allows shedding of lianas (Talley *et al.*

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1996). In contrast, contrary to smooth bark, rough bark can increase liana infestation (Carse *et al.* 2000; Carsten *et al.* 2002; Reddy & Parthasarathy 2006; Talley *et al.* 1996) because it provides a suitable surface for liana attachment (Talley *et al.* 1996).

Another tree characteristic related to climber infestation is height, which may be a consequence of three non-exclusive processes: (a) liana relay ascent (Pinard & Putz 1994), (b) taller trees are generally older and have had more time to accumulate lianas (Campanello *et al.* 2007; Malizia & Grau 2006; Pérez-Salicrup *et al.* 2001), and (c) larger trees intercept more light than shorter trees, providing an ideal environment for light-loving lianas (Malizia & Grau 2006). Many studies demonstrate that taller trees bear more lianas and understory trees are less prone to host lianas (Carrasco-Urra & Gianoli 2009; Clark & Clark 1990; Ding & Zang 2009; Jimenez-Castillo & Lusk 2009).

While single attributes of trees may facilitate or repel liana infestation, a combination of attributes may be more effective against liana occupation (Carse *et al.* 2000). For instance, trees with smooth bark and flexible stems (Carse *et al.* 2000) or short trees with more shaded canopies are less prone to liana infestation (Sfair *et al.* 2013). A spectrum of traits can provide a continuum of trees more prone or less prone to carry lianas (Sfair *et al.* 2010).

Here, we evaluate four tree attributes that purportedly are related to lower liana infestation: (1) lower height (Carrasco-Urra & Gianoli 2009; Clark & Clark 1990; Ding & Zang 2009; Jimenez-Castillo & Lusk 2009), (2) exfoliating bark (Campanello *et al.* 2007; Talley *et al.* 1996), (3) early successional status (Campanello *et al.* 2007; Carse *et al.* 2000; Clark & Clark 1990), and (4) smooth bark (Carse *et al.* 2000; Carsten *et al.* 2002; Reddy & Parthasarathy 2006; Talley *et al.* 1996). We pose the question: Does the presence of multiple tree attributes reduce the number of lianas on a tree? We predict that tree individuals with combined attributes, such as a small tree with exfoliating bark, are less prone to carry several lianas than trees with a single attribute.

## Materials and methods

We sampled lianas and trees rooted in 1 ha plots at three sites in the state of São Paulo, southeast Brazil. Each site has a distinct vegetation type, to which different sampling designs

were applied, taking into account the specifics of each community, such as average height, diameter, and density of lianas and trees. For example, the savanna woodland has shorter, smaller diameter trees than rain forest; hence, the minimum diameter at breast height (dbh) we measured was 3 cm, versus 5 cm in rain forest. Lianas and trees of the three areas had been previously sampled for other purposes, e.g., general community analyses, so this limited the selection of variables available for our study. For example, we do not have data on the branch-free bole height for either seasonal forest or savanna woodland, an attribute that may influence liana occupancy (Campanello *et al.* 2012).

The rain forest site (23° 21' 54" - 23° 21' 59" S, 45° 05' 02" - 45° 05' 04" W, 348 - 394 m asl) is a part of the Brazilian Atlantic forest in the municipality of Ubatuba, in the Parque Estadual da Serra do Mar. Ubatuba has a humid tropical climate with no distinct dry season, and no month with rainfall less than 60 mm (Rochelle *et al.* 2011; van Melis 2008; Table 1).

The seasonal forest site (19°55' - 19°58' S, 49° 31' - 49° 32' W, 400 - 495 m asl) is also part of the Brazilian Atlantic forest and is located in the municipality of Paulo de Faria. This forest experiences distinct precipitation seasonality (Rezende *et al.* 2007), with precipitation during the driest months ranging from 5 to 20 mm. Plots with densely tangled lianas were excluded (Rezende *et al.* 2007; Table 1).

The savanna woodland site (22° 19' 41" - 21° 06" S, 48° 59'49" - 49° 01' 12" W, 519 - 603 m asl) is a cerrado forest, characterized by the presence of taller trees and a low density of shrubs, in the municipality of Bauru. This is also a seasonal forest, with precipitation occurring mainly between September and May. The precipitation of the driest month is 20 to 40 mm (Weiser 2007; Table 1).

For all sites and individuals, we recorded tree structural attributes derived from the literature that may diminish liana occupation (e.g., Clark & Clark 1990; Campanello *et al.* 2007; Carse *et al.* 2000; Putz 1984). We only considered the individual level for trees, because species identity is a weak predictor of liana occupancy (Malizia & Grau 2006; Sfair *et al.* 2010) and tree attributes can vary intra-specifically. We recorded host plant (1) height (H); (2) exfoliating bark (EB); (3) fast growth (FG; *sensu* Swaine & Whitmore 1988); and (4) smooth bark (SB). Height was a continuous variable, whereas exfoliating bark and fast growth

were binary variables (presence and absence), and bark roughness was a categorical variable (smooth, intermediate and rough). Height and exfoliating bark were recorded for all three sites, whereas fast growth was only recorded for seasonal and rain forest sites, and smooth bark for savanna woodland only. Fast growth was not used to analyze the savanna woodland because cerrado vegetation dynamics are generally not determined by light availability (Coutinho 1978). Instead, we used bark roughness, because it is a typical characteristic of cerrado plants: rough bark is associated with low mortality of aerial organs following fire (Hoffman *et al.* 2009), while trees with smooth bark are reportedly less prone to host lianas in cerrado vegetation (Weiser 2007). Tree height, presence of exfoliating bark, and bark roughness were recorded in the field, whereas fast growth information was derived from the literature (Lorenzi 1998) and personal knowledge. The identity of trees and liana species was not considered in the statistical analyses. Other morphological attributes and potential mechanisms for liana exclusion, such as presence of spines and bole free height, were not included here, because we lacked data for trees from at least two sites.

We compared the number of trees with exfoliating bark, smooth bark, and fast growth in each site separately using a chi-square test, whereas tree height was compared using regression with Poisson distribution, a type of generalized linear model (GLM; Crawley 2007). In this model, the number of lianas on a host plant was considered a response variable, whereas height was the independent variable. The data were overdispersed in seasonal forest and savanna woodland; therefore, we used the quasi-Poisson instead of Poisson distribution (Crawley 2007).

We also used GLM with Poisson distribution to predict the probability of the number of lianas per tree as a function of the tree attributes described above. Again, the number of lianas on a host plant was considered a response variable, whereas height, exfoliating bark, fast growth and bark roughness were explanatory variables. Using these variables, we built models with one, two, and three tree explanatory variables. To select the best statistical model, we calculated the Akaike Information Criterion (AIC) for all possible models. AIC is founded in maximum likelihood, in which multiple competing hypotheses are tested and, based on model parsimony, the best statistical models are the ones with lower values of AIC

(Anderson 2008; Burnham & Anderson 2002; Johnson & Omland 2004; Mazerolle 2006).

We used the corrected AIC for small samples (AICc), which approaches the AIC when the sample is large (Mazerolle 2006). To compare different models, we calculated the  $\Delta\text{AICc}_i$ , a measure of each model relative to the best model:  $\Delta\text{AICc}_i = \text{AICc}_i - \text{minAICc}$ , where  $\text{AICc}_i$  is the AICc value for model  $i$  and  $\text{minAICc}$  is the AICc value for the best model (Mazerolle 2006). A lower  $\Delta\text{AICc}$  - lower than two, for example - offers substantial evidence in favor of both models; intermediate values (between three and seven) indicate that the model has considerably less support. However, higher difference values, such as those higher than ten, show that the model is very unlikely when compared to a model with a lower AICc (Burnham & Anderson 2002). Additionally, we calculated the Akaike weights ( $w$ ), which represent the ratio of the  $\Delta\text{AICc}$  of a given model in relation to the complete set of candidate models, to demonstrate the likelihood of a model being the best among the set (see Mazerolle 2006 for formulae). For example,  $w = 0.64$  indicates that this model has a 64 % chance of being the best among all models considered. We performed these analyses on the *glmulti* package in R (Calcagno 2013). For the rain forest and seasonal forest, data were overdispersed, i.e.,  $\hat{c}$  ( $\chi^2/\text{df}$ ; where  $\hat{c}$  is the overdispersion parameter,  $\chi^2$  is the goodness-of-fit test statistic based on the global model, and  $\text{df}$  is the degrees of freedom of the test) of the most complete model was higher than one ( $\hat{c} = 2.05$  and  $\hat{c} = 3.27$ , respectively, whereas  $\hat{c} = 0.94$  in the savanna woodland). For this reason, we used the modified QAICc for the models of tree-liana association for these two sites (Anderson 2008).

## Results

The three forests showed strong differences in liana and tree abundances, with the rain forest having the lowest abundance of liana individuals (Table 1). Taller trees hosted more lianas in all three sampled areas (Fig. 1, Table 2). Most of the trees did not have exfoliating bark in the rain forest (81.3 %) and woodland savanna (85.3 %) (Fig. 2a, c). However, in seasonal forest, in spite of most of trees bearing persistent bark (70.1 %), trees with exfoliating bark had less lianas (Fig. 2b, Table 2). Slow growth was found in 78.8 % and 73.5 % of the trees in the rain forest and the seasonal forest, respectively. Rain forest trees scored as “fast growth” hosted a lower number of

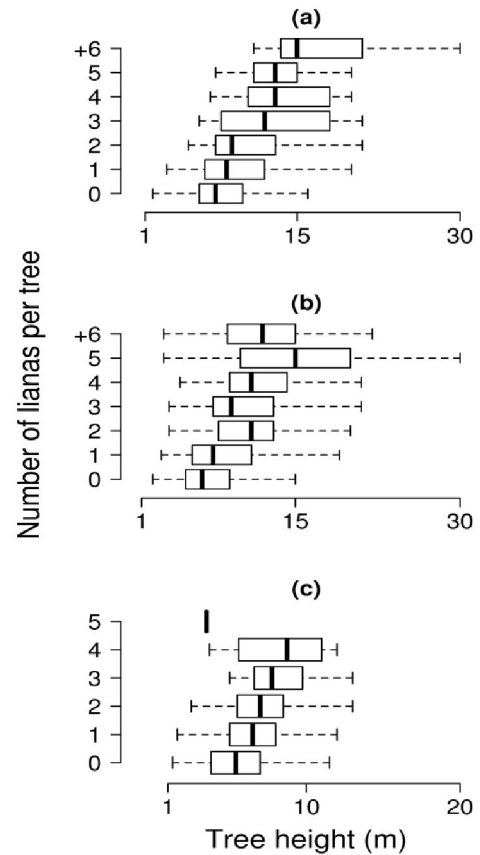
**Table 1.** Abundance of trees and lianas, and the percentage of trees with lianas in rain forest, seasonal forest, and savanna woodland. For the three vegetation types, 1 ha areas were sampled. dbh = diameter at breast height; dsh = diameter at soil height.

	Rain forest	Seasonal forest	Savanna woodland
Abundance of trees (ha <sup>-1</sup> )	1878	1419	2967
Diameter of trees measured (dbh ≥ (cm))	5	3	3
Trees with lianas (ha <sup>-1</sup> )	350 (18.6 %)	873 (61.5 %)	1141 (38.4 %)
Abundance of lianas (ha <sup>-1</sup> )	526	1427	859
Diameter of lianas measured (cm)	dbh ≥ 1	dbh ≥ 1	dsh ≥ 1
Details on sampling	van Melis 2008; Rochelle <i>et al.</i> 2011	Rezende <i>et al.</i> 2007	Weiser 2007

lianas (Fig. 2d) but in the seasonal forest, fast growth status did not influence the number of lianas that a tree hosted (Fig. 2e, Table 2). In the savanna woodland, 53.2 % of the trees had intermediate bark roughness, 33.4 % had smooth bark, and 13.4 % had rough bark. Trees that hosted significantly more lianas had intermediate or rough bark texture (Fig. 2f, Table 2).

In all three forest areas analyzed, the best model with a single independent variable included height, but had no probability of being the best model (Table 3). Conversely, the probability was greater than 65 % of models with two variables being the best model for all three sites. The combination of three attributes was as efficient as the combination of two traits in repelling lianas on a tree for all three sites (Table 3, all cases  $\Delta(Q)AICc < 2$ ). For all sites, the best multi-trait model always included height (Table 3).

In rain forest, the model with a combination of height and fast growth status was the best ( $Q_w = 0.73$ ), but the combination of height, fast growth, and exfoliating bark, was also a good model ( $\Delta AICc < 2$ ; Table 3). In seasonal forest, the combination of height and exfoliating bark formed the best model



**Fig. 1.** Taller trees bear more lianas in all sampled forest types (rain forest (a), seasonal forest (b) and savanna woodland (c)). Symbols for each number of lianas show, from left to the right, minimum, first quartile, median, third quartile, and maximum.

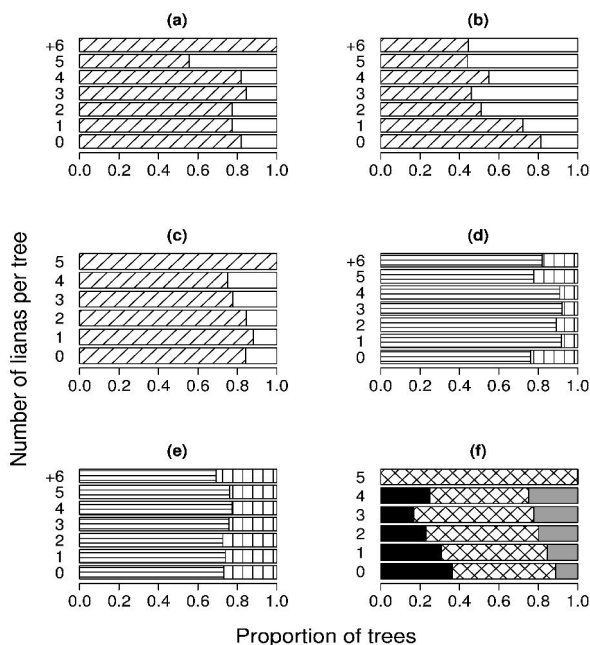
( $Q_w = 0.65$ ), but the presence of a third attribute in the model also influenced liana number ( $\Delta QA ICc < 2$ ; Table 3). In savanna woodland, a combination of two tree attributes was correlated with the number of lianas: the best model included height and smooth bark ( $w = 0.71$ ; Table 3).

## Discussion

Trees with attributes such as low height, smooth bark, or exfoliating bark may be subject to lower infestation by lianas. Whereas a single attribute can deter liana climbing (Campanello *et al.* 2007; Putz 1984), in the three different vegetation types analyzed in this study, a combination of attributes was better at predicting the number of lianas on a tree than was one attribute. In fact, our results indicate that two attributes of a tree are sufficient to influence liana colonization, and the addition of a third attribute has less impact on

**Table 2.** Comparisons among liana number on trees relative to tree height (H), exfoliating bark (EB), fast growth status (FG), and smooth bark (SB) for rain forest, seasonal forest, and savanna woodland in southeast Brazil. In these cases, the number of lianas on a tree was the dependent variable, and the attributes were the independent variables. Analyses were independent from one other. For height, we used regression with Poisson distribution. For exfoliating bark, fast growth status, and smooth bark, we used a Chi-square test.  $\chi^2$  is the value of the Chi-square test, and df is the degrees of freedom (df). \*denotes  $P < 0.05$ .

	Rain forest		Seasonal forest		Savanna woodland	
	$\chi^2$	df	$\chi^2$	df	$\chi^2$	df
H	150*	1	110*	1	151*	1
EB	10.4	11	123*	19	9.97	5
FG	38.7*	11	16.3	19	-	-
SB	-	-	-	-	35.2*	10



**Fig. 2.** Number of lianas per tree with (white) and without (shading lines) exfoliating bark in the rain forest (a), seasonal forest (b), savanna woodland (c); fast growth (horizontal lines) and non-fast growth (vertical lines) in rain forest (d) and seasonal forest (e). For bark roughness (f), shown are number of lianas per tree with smooth (black), intermediate level (crossed lines), and rough bark (grey) in savanna woodland only.

liana climbing: the analyses of this third attribute separately showed that its presence was non-significant, regardless of vegetation type (Table 2). For instance, in the rain forest, height and fast growth were the attributes present in the best model (Table 3), but they also influenced the number of lianas on a tree when analyzed separately

(Table 2). On the other hand, the presence of three attributes (short tree, fast growth status, and exfoliating bark) were associated with trees with fewer numbers of lianas (Table 3). However, the third attribute (exfoliating bark) was not correlated with the number of lianas when evaluated alone (Table 2). For this reason, we base the following discussion only on the best and simplest models, i.e., those with two predictor variables.

In all three vegetation types, tree height was significantly correlated with the number of lianas: taller trees bear more lianas. Three processes may explain this relationship. First, many lianas may climb each other and together reach the canopy of large trees. Therefore, once a liana climbs a tall tree, other lianas may take advantage of this shortcut (Pinard & Putz 1994). Second, taller trees are generally older and have had more time to accumulate lianas (Campanello *et al.* 2007; Malizia & Grau 2006; Pérez-Salicipup *et al.* 2001). Third, larger trees intercept more light than shorter trees, providing an ideal environment for light-loving lianas (Malizia & Grau 2006; Sfair *et al.* 2013).

Light requirements of a liana species may vary due to phenotypic plasticity or genetic differentiation (Gianoli *et al.* 2012), which may explain the lack of significant relationship between the abundance of lianas and light in temperate forests (Carrasco-Urra & Gianoli 2009). Nevertheless, in tropical forests, lianas can be abundant in disturbed and more enlightened areas (Mohandass *et al.* 2015). In a seasonal tropical Atlantic forest, both tree height and canopy exposure to light influence the probability of infestation by lianas. In this case, taller trees also have canopies more exposed

**Table 3.** Three most parsimonious models and their respective variables. The independent variables were the attributes (H, EB, FG, EB) and the dependent variable was the number of lianas on a tree. For rain forest and seasonal forest, we calculated QuasiLL, QAICc,  $\Delta$ QAICc and Qw. For woodland savanna, we calculated LL, AICc,  $\Delta$ AICc and w. H = height; EB = exfoliating bark; FG = fast growth; SB = smooth bark.

Model				K	(Quasi) LL	(Q) AICc	$\Delta$ (Q)AICc	(Q)w
Rain forest								
FG	+	H		5	-699.96	1409.95	0.00	0.73
EB	+	FG	+ H	6	-699.94	1411.92	1.97	0.27
H				3	-709.42	1424.86	14.91	0.00
Seasonal forest								
EB	+	H		4	-803.99	1616.00	0.00	0.65
EB	+	FG	+ H	5	-803.59	1617.22	1.22	0.35
H				3	-827.63	1661.28	45.28	0.00
Savanna woodland								
SB	+	H		4	-2606.52	6065.00	0.00	0.71
EB	+	SB	+ H	5	-2606.2	6066.77	1.77	0.29
H				2	-2618.03	6087.51	22.51	0.00

to light and are more prone to carry lianas (Sfair *et al.* 2013). Therefore, in our study, height may be a proxy for crown light availability.

Light availability can be the principal factor influencing liana occupation on trees and the presence of other attributes alone, such as exfoliating bark, taller free bole height, and smooth bark, are not sufficient to diminish lianas infestation (Sfair *et al.* 2013). Our results indicate that a second tree attribute does play a role in liana occupancy and the attribute varies according to the type of vegetation: fast growth status in the rain forest, exfoliating bark in the seasonal forest, and bark roughness in the savanna woodland. In the rain forest, our data corroborated previous research that showed climax species hosting more lianas (Campanello *et al.* 2007; Carrasco-Urra & Gianoli 2009; Carse *et al.* 2000; Clark & Clark 1990; Ding & Zang 2009; Jimenez-Castillo & Lusk 2009). Fast growth species germinate primarily after gap creation, in contrast to slower growing or climax species, whose seeds can germinate under the forest shade (Swaine & Whitmore 1988). Our rain forest sample was in mature forest without gaps, which may have influenced the fact that almost 80 % of the trees were slow growing and still hosted lianas.

The importance of bark attributes on liana occupancy partially corroborated our predictions in seasonal forest and woodland savanna. In seasonal forest, equal proportions of trees with exfoliating and persistent bark hosted more than two lianas

whereas more than 70 % of trees with persistent bark had one liana. These results are contrary to our expectations, in which trees with exfoliating bark would have fewer lianas. This attribute seems to be a weak predictor of liana occupancy: Carsten *et al.* (2002) showed that liana colonization is higher on trees with intermediate levels of exfoliating bark, whereas Sfair *et al.* (2013) showed that exfoliating bark does not influence liana climbing. Therefore, we suggest that this attribute be considered carefully in future studies addressing liana-tree associations. Probably other attributes, such as canopy exposure to light, are better predictors of liana colonization on a tree than presence of exfoliating bark.

Our data indicate that savanna woodland bark roughness does influence liana-host association: intermediate and rough bark are associated with more lianas, whereas smooth bark is associated with fewer lianas. This result may vary with vegetation type: in a tropical forest, smooth bark is not related to exclusion of lianas (Boom & Mori 1982). The divergence of the importance of bark roughness between a tropical forest and a savanna woodland is probably due to the diversity of bark types in savanna, which covers a broader spectrum: from very smooth bark to deeply fissured (Weiser 2007). The high levels of roughness are associated with fire protection (Hoffman *et al.* 2009) and significantly reduce the duration of radiation, thus decreasing the temperature in a bark valley or under a bark plate by shading

(Nicolai 1986). High levels of bark roughness, found in cerrado tree species, are also associated with colonization by mistletoe (Arruda *et al.* 2006) and lichen (Mistry & Berardi 2005), indicating the importance of this attribute to other organisms.

## Conclusions

Single attributes were less effective in deterring lianas than a combination of two or three attributes. One consistently important variable is tree height: taller trees are more likely to host lianas and, for the three sites sampled, height is always associated with another attribute, such as exfoliating bark, fast growth status, or smooth bark in trees with high numbers of lianas. Nevertheless, the importance of tree height to liana colonization and climbing seems to be associated with light availability, while the other attribute plays a minor role. The exception is in open savanna woodland vegetation, where smooth bark is associated with fewer lianas on trees. The importance of light for liana climbing, relative to the vegetation structure, deserves further investigation.

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## References

- Anderson, D. R. 2008. *Model Based Inference in the Life Sciences- a Primer on Evidence*. Springer, New York.
- Arruda, R., L. N. Carvalho & K. Del-Claro. 2006. Host specificity of a brazilian mistletoe, *Struthanthus aff. polyanthus* (Loranthaceae), in cerrado tropical savanna. *Flora - Morphology, Distribution, Functional Ecology of Plants* **201**: 127-134.
- Boom, B. M. & S. A. Mori. 1982. Falsification of two hypotheses on liana exclusion from tropical trees possessing buttresses and smooth bark. *Bulletin of the Torrey Botanical Club* **109**: 447-450.
- Burnham, K. P. & D. R. Anderson. 2002. *Model Selection and Multi-Model Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Calcagno, V. 2013. *Glmulti: Model Selection and Multi-model Inference Made Easy*. R package version 1.0.7. <http://CRAN.R-project.org/package=glmulti>
- Campanello, P. I., J. F. Garibaldi, M. G. Gatti & G. Goldstein. 2007. Lianas in a subtropical Atlantic forest: host preference and tree growth. *Forest Ecology and Management* **242**: 250-259.
- Campanello, P. I., M. Villagra, J. F. Garibaldi, L. J. Ritter, J. J. Araujo & G. Goldstein. 2012. Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. *Forest Ecology and Management* **284**: 213-221.
- Carrasco-Urra, F. & E. Gianoli. 2009. Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability? *Journal of Vegetation Science* **20**: 1155-1162.
- Carse, L. E., T. S. Fredericksen & J. C. Licona. 2000. Liana-tree species associations in a Bolivian dry forest. *Tropical Ecology* **41**: 1-10.
- Carsten, L. D., F. A. Juola, T. D. Male & S. Cherry. 2002. Host associations of lianas in a south-east Queensland rain forest. *Journal of Tropical Ecology* **18**: 107-120.
- Clark, D. B. & D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemi-epiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* **6**: 321-331.
- Coutinho, L. M. 1978. O conceito de cerrado. *Revista Brasileira de Botânica* **1**: 17-23.
- Crawley, M. J. 2007. *The R Book*. John Wiley & Sons Ltd., Chichester.
- DeWalt, S. J., S. A. Schnitzer, J. Chave, F. Bongers, R. J. Burnham, Z. Cai, G. Chuyong, D. B. Clark, C. E. N. Ewango, J. J. Gerwing, E. Gortaire, T. Hart, G. Ibarra-Manríquez, K. Ickes, D. Kenfack, M. J. Macía, J. R. Makana, M. Martínez-Ramos, J. Mascaro, S. Moses, H. C. Muller-Landau, M. P. E. Parren, N. Parthasarathy, D. R. Pérez-Salicrup, F. E. Putz, H. Romero-Saltos & D. Thomas. 2009. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* **42**: 309-317.
- Ding, Y. & R. Zang. 2009. Effects of logging on the diversity of lianas in a lowland tropical rain forest in Hainan Islands, South China. *Biotropica* **41**: 618-624.
- Fonseca, M. G., E. Vidal & F. A. M. Santos. 2009. Intraspecific variation in the fruiting of an Amazonian timber tree: implications for management. *Biotropica* **41**: 179-185.
- Gianoli, E., A. Saldaña & M. Jiménez-Castillo. 2012. Ecophysiological traits may explain the abundance of climbing plant species across the light gradient in

- a temperate rainforest. *PloS One* **7**: e38831.
- Grogan, J. & M. Landis. 2009. Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. *Journal of Applied Ecology* **46**: 1283-1291.
- Hegarty, E. E. 1991. Vine-host interactions. pp. 357-376. In: F. E. Putz & H. A. Mooney (eds.) *The Biology of Vines*. Cambridge University Press, Cambridge.
- Hoffmann, W. A., R. Adasme, M. Haridasan, M. T. De Carvalho, E. L. Geiger, M. A. B. Pereira, S. G. Gotsch & A. Franco. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* **90**: 1326-1337.
- Jiménez-Castillo, M. & C. H. Lusk. 2009. Host infestation patterns of the massive liana *Hydrangea serratifolia* (Hydrangeaceae) in a Chilean temperate rainforest. *Austral Ecology* **34**: 829-834.
- Johnson, J. B. & K. S. Omland. 2004. Model selection in ecology and evolution. *Evolution* **19**: 101-108.
- Lorenzi, H. 1998. *Árvores Brasileiras: Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil*. Vols. 1-3. Editora Plantarum, Nova Odessa.
- Malizia, A. & H. R. Grau. 2006. Liana-host tree associations in a subtropical montane forest of north-western Argentina. *Journal of Tropical Ecology* **22**: 331-339.
- Mazerolle, M. J. 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* **27**: 169-180.
- Mistry, J. & A. Berardi. 2005. Effects of phorophyte determinants on lichen abundance in the cerrado of central Brazil. *Plant Ecology* **178**: 61-76.
- Mohandass, D., P. Davidar, S. Somasundaram, L. L. Vijayan & K. C. Beng. 2015. Influence of disturbance regime on liana species composition, density and basal area in the tropical montane evergreen forests (sholas) of the western ghats, India. *Tropical Ecology* **56**: 169-182.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* **69**: 148-160.
- Pérez-Salicip, D. R., V. L. Sork & F. E. Putz. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* **33**: 34-47.
- Pinard, M. A. & F. E. Putz. 1994. Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: biomechanical facilitation in vine succession. *Journal of Tropical Forest Science* **6**: 302-309.
- Putz, F. E. 1984. How trees avoid and shed lianas. *Biotropica* **16**: 19-23.
- Reddy, M. S. & N. Parthasarathy. 2006. Liana diversity and distribution in four inland tropical dry evergreen forests of peninsular India. *Tropical Ecology* **47**: 109-123.
- Rezende A. A., N. T. Ranga & R. A. S. Pereira. 2007. Lianas de uma floresta estacional semidecidual, Município de Paulo de Faria, Norte do Estado de São Paulo, Brasil. *Revista Brasileira de Botânica* **30**: 451-461.
- Rochelle, A. L. C., R. Cielo-Filho & F. R. Martins. 2011. Tree community structure in an Atlantic forest fragment at Serra do Mar State Park, southeastern Brazil. *Biota Neotropica* **11**: 337-346.
- Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* **166**: 262-276.
- Sfair, J. C., B. R. Ribeiro, E. P. Pimenta, T. Gonçalves & F. N. Ramos. 2013. A importância da luz na ocupação de árvores por lianas. *Rodriguésia* **64**: 255-261.
- Sfair, J. C., A. L. C. Rochelle, A. A. Rezende, J. van Melis, V. L. Weiser & F. R. Martins. 2010. Nested liana-tree network in three distinct neotropical vegetation formations. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 277-281.
- Swaine, M. D. & T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**: 81-86.
- Talley, S. M., W. N. Setzer & B. R. Jackes. 1996. Host associations of two adventitious-root-climbing vines in a North Queensland Tropical Rain Forest. *Biotropica* **28**: 356-366.
- van Melis, J. 2008. *Lianas: Biomassa em Floresta Neotropical e Relação Riqueza e Biomassa em um Trecho de Floresta Ombrofila Densa Atlântica*. M.Sc. dissertation, Universidade Estadual de Campinas, Campinas, São Paulo.
- Violle, C., M. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier. 2007. Let the concept of trait be functional! *Oikos* **116**: 882-892.
- Weiser, V. L. 2007. *Árvores, Arbustos e Trepadeiras do Cerradão do Jardim Botânico Municipal de Bauru, SP*. Ph.D. Dissertation, Universidade Estadual de Campinas, Campinas, São Paulo.

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